Brood parasitism by cowbirds: risks and effects on reproductive success and survival in indigo buntings

Robert B. Payne[a,b] **and Laura L. Payne**[a]
[a]Museum of Zoology and [b]Department of Biology, University of Michigan, Ann Arbor, MI 48109-1079, USA

We observed brood parasitism by brown-headed cowbirds (*Molothrus ater*) on indigo buntings (*Passerina cyanea*) and estimated the impact of parasitism on the success of the individual buntings in their current nests and in their future survival and reproduction. Rates of parasitism over 8 years were 26.6% in 1040 nests and 19.8% in 693 nests in two areas in southern Michigan. Risk of parasitism was high early in the season; half the bunting nests were begun after the end of the cowbird season. Risk was independent of female age, plant containing the nest, or habitat. The immediate cost of parasitism was 1.19 and 1.26 fewer buntings fledged per nest. Bunting success was lower in parasitized nests with cowbird eggs (nests were more likely to be deserted or predated), lower when the cowbird nestling failed (nests were more likely to be predated), and lower when the cowbird fledged (fewer buntings fledged) compared to nonparasitized nests. Costs were due to removal of a bunting egg when the cowbird laid its own egg and to competition for parental care of the cowbird and bunting nestlings. Buntings that fledged from nests where a cowbird also fledged were only 18% as likely to survive and return to their natal area in the next year as buntings from nests where a cowbird did not fledge. Long-term effects of cowbird parasitism on adult breeding later in the season, survival to the next season, and reproductive success in the next season were negligible when compared between birds that reared a cowbird and birds that reared only a bunting brood, or between birds that were parasitized and birds that escaped parasitism. The results indicate little long-term cost of brood parasitism on individual fitness of adult buntings beyond the impact on the current nest and the survival of buntings that fledge from it; nearly all cost is to the parasitized brood. *Key words:* breeding seasons, brood parasitism, brown-headed cowbirds, cost of parasitism, cost of reproduction, indigo buntings, individual fitness, *Molothrus ater*, natal philopatry, nest predation, nestling competition, *Passerina cyanea*, postfledging survival, reproductive success. *[Behav Ecol 9:64–73 (1998)]*

Brood parasitism is the breeding style of nearly 100 species of birds that regularly lay their eggs in the nest of another species, the host, which rears their young. Brood parasitic cowbirds lower the breeding success of their hosts when the female cowbird removes a host egg from the nest and when the cowbird nestling competes for parental care with the host brood. Estimates on a nest-by-nest basis of the effect of cowbird parasitism on breeding success are available for several host species of the North American brown-headed cowbird (*Molothrus ater*) (Friedmann, 1963; Lowther, 1993; Nice, 1937; Payne, 1977, 1997; Rothstein, 1975, 1990; Smith, 1981a). The risk of parasitism may vary among individual birds with habitat and nest site differences, age, and experience, and the impact of parasitism may vary with the stage of nesting, with consequences on the evolutionary options for defense against the adult cowbirds and their eggs and young. In addition to egg removal and nestling competition, there may also be a significant postfledging effect on the host young when reared together with a cowbird, so that even fledging may not lead to recruitment of the offspring into the breeding population. Although the costs of brood parasitism have been estimated from the proportion of nests parasitized and the lower production of host young from these nests, it is not known whether being parasitized affects the later reproductive success and survival of the individual foster parents.

Because rearing a cowbird might affect the later reproduction and survival of the foster parents (May and Robinson, 1985), it is of interest to determine whether their future performance is lowered when they rear a cowbird compared with when they rear only their own brood. In addition to the costs on their current nest, rearing a cowbird might decrease the probability of their nesting again and might decrease the success of their later brood in the season, and there might be a long-term cost to the adult foster parents in terms of survival and reproductive success in the next season.

The schedule of costs of parasitism may affect the evolutionary responses of the hosts to brood parasitism. Many songbirds leave the cowbird egg in their nest ("acceptors") rather than removing it or deserting the nest ("rejecters") (Rothstein, 1990). More songbird hosts in the New World accept a cowbird egg than in the Old World where songbirds are parasitized by cuckoos. The difference may be that cowbirds have less effect on their hosts' breeding success after their eggs are laid than cuckoos do: the nestling cuckoo evicts all the eggs and nestlings from the nest, whereas the nestling cowbird is more benign; in some hosts a nest mate may survive to fledge with the cowbird (Payne, 1997). If non-recoverable costs due to removal of a host egg by a cowbird parasite are the main source of loss (Røskaft et al. 1990), in contrast to parasitism by cuckoos, when most loss occurs after the nestling hatches, then response may be limited. On the other hand, if long-term costs on survival and reproduction of the breeding adult hosts are significant, then response may be even greater than expected from the effect of a cowbird on the current nest.

The effort of rearing a brood parasite may affect the future success of the breeding hosts, much as rearing a large brood of their own may affect their physiological condition and reproductive value. The hypothesis of a cost of reproduction proposes that the effort in breeding affects the condition of a breeder and lowers its survival and reproductive success in

later breeding attempts (Lessells, 1991; Partridge, 1989; Reznick, 1985; Stearns, 1992; Williams, 1966;). Observations and experimental tests give some support for this hypothesis. For example, great tits (*Parus major*) that rear larger broods early in the season are less likely to have a second brood within the same season (Perrins, 1965). House sparrows (*Passer domesticus*) that rear larger broods early in the season have smaller broods later in the season (McGillivray, 1983). Rooks (*Corvus frugilegus*) and pied flycatchers (*Ficedula hypoleuca*) that rear enlarged broods in one season have lower reproductive success in the next season (Gustafsson and Pärt, 1990; Gustafsson and Sutherland, 1988; Røskaft, 1985). Finally, blue tits (*Parus caeruleus*) that rear enlarged broods have lower survival into the next season (Pettifor, 1993). In other studies, the birds that rear a naturally large brood or an experimentally enlarged brood sometimes not show a lower survival or reproductive success (Högstedt, 1981; Lessells, 1993; Lindén and Møller, 1989; Nur, 1988; Orell et al., 1996; Partridge, 1989; Smith, 1981b; Wheelwright et al., 1991; Winkler and Wilkinson, 1988; Verhulst and Hut, 1996).

We observed brood parasitism of brown-headed cowbirds on the indigo bunting (*Passerina cyanea*), a small songbird of eastern North America. We determined the effect of cowbird parasitism on the reproductive success of individual birds at each nest and through the breeding season, their survival and reproductive success in the next year, and survival of their fledglings to the next year. If parasitism affects the ability of a bunting to rear a later brood, then we predict that fewer nests will be started after a parasitized nest than after an unparasitized nest of the pair and that earlier parasitism will affect the success of the later nest, especially when the earlier nest was successful and a cowbird fledged. If rearing a cowbird affects the survival of adult buntings, then we predict that fewer buntings will return in the year after they fledged a cowbird than after they fledged only their own brood or failed to rear any brood. Finally, if rearing a cowbird affects reproductive success in a later year, then we predict that fewer buntings will be fledged in the following year. For this prediction we tested the female buntings, as they provide the parental care to the time of fledging and are the sex most likely to show a cost of parasitism.

METHODS

Study areas, populations, and reproductive success

We observed indigo buntings in southern Michigan, USA (Payne, 1989, 1992; Payne and Payne, 1990, 1993a,b; Payne et al., 1988). We color banded the breeding birds and found nearly all nests in two study areas, one near Niles (41°55' N, 86°14' W) was 4 km², the other at the E. S. George Reserve and neighboring lands (42°27' N, 84°00' W) was 12 km². We located the position of each male, the territory occupied, and all nests on maps and a series of aerial photographs of the study areas.

For each male we categorized the territory according to whether it occupied one of five major habitats: upland woods (oak *Quercus* spp.), mesic woods (sugar maple *Acer saccharum*, aspen *Populus grandidentata*), black locust *Robinia pseudoacacia* thickets, upland old fields, swamp, or edge of field and woods, as determined by field observations and aerial photographs. Bunting nests generally were within 1.2 m of the ground under the canopy of a dense herb or shrub. We identified 38 kinds of plants in which the nests were built; most were in shrubs of black raspberry (*Rubus occidentalis*) or gray dogwood (*Cornus racemosa*) and others with 10 or more nests were in saplings especially maple, in shrubs (staghorn sumac *Rhus typhina*, multiflora rose *Rosa multiflora*, gooseberry *Ri-*

bes cynosbati, honeysuckle *Lonicera* spp.), and in low herbs (bracken *Pteridium aquilinum*, goldenrod *Solidago* spp.). We compared the proportion of nests parasitized by cowbirds in these habitats and nest plants.

We determined the date of the first egg in each nest. The earliest egg in any year was laid on 14 May; the latest date for nestlings was 7 September. Nest building took up to 8 days in early spring but sometimes only 2 days in summer. Clutch size was usually three or four. The incubation period was 12–14 days for buntings and 11 days for cowbirds. Young buntings and cowbirds remained in the nest for 9–10 days, or a few days longer (up to 14 days) in cool weather. Female buntings bred in their first year, built the nest, incubated, and fed the nestlings; reproductive success was independent of female age (Payne, 1989). Males bred in their first year and many were successful, though the older adults were more successful. Males often fed the young after they fledged (Westneat, 1988) and also fed the fledged cowbirds (Sutton, 1959). Females frequently renested after the loss of an earlier nest and attempted as many as seven nests, and they often reared two broods and occasionally three broods in a season. Breeding pairs were active for as long as 14 weeks.

We captured the males in mist nets on their territories, then measured, weighed, and color banded them and aged them by plumage: the greater primary coverts were brown in yearlings (first-year males) and blue in older adult males. We found no plumage differences between yearling and older adult females, but we knew the ages of females that we had banded as nestlings and the minimum ages of females that we had banded in an earlier year. We banded nearly all territorial male buntings and about half the females with a U.S. Fish and Wildlife (USFWS) band and three color bands for individual recognition. Males were 12.5–17.5 g ($n = 1,159$, $\bar{x} = 14.96 \pm 0.74$ g). Females were 11.9–17.5 g ($n = 398$, $\bar{x} = 14.33 \pm 0.96$ g). Cowbird adults were larger than buntings (males, $n = 32$, $\bar{x} = 49.62 \pm 4.07$ g; females, $n = 27$, $\bar{x} = 39.14 \pm 2.80$ g), nestlings were as large as 33.1 g, and fledglings being fed by a host were as large as 38.0 g (cowbird specimens from southern Michigan in the University of Michigan Museum of Zoology).

We determined the immediate effect of cowbirds on reproductive success from the nesting and fledging success of buntings from 1980 through 1987. We censused each territory at least once a week through the breeding season. When we saw a female with nesting material in her bill or knew that she was mating or laying, we avoided the site so that we would not cause her to desert the nest. We compared breeding success for 1733 bunting nests which met the following criteria: (1) a bird (cowbird or bunting) laid at least one egg, (2) the male was born by 1984 (we did not follow all birds in later years, though the birds born from 1979 through 1984 we followed through 1991) or the male or its mate was banded as a nestling or was known to be the parent of a nestling that returned to its natal area, (3) we did not disturb the nest (that is, we did no apparent damage to the nest or its contents, such as when we accidentally trampled a few nests or spilled a nest and broke the eggs, or we netted the female within a few days after she laid and she then deserted, or she deserted her young when she was biopsied; Westneat et al., 1986; $n = 13$, or 1% of all nests), and (4) we determined nesting and fledging success by visiting the nest until it failed or fledged. We compared the frequency of nest parasitism with age of the breeding adult to test whether parasitism decreased with age and breeding experience.

We identified the eggs and nestlings by their appearance. Cowbird eggs were large (20–23×15–17 mm) and pale blue with brown spots; indigo bunting eggs were small (17–20×13–15 mm), white and unspotted. Cowbird nestlings were large

and had pink mouth linings, a white gape, and gray-white natal down; bunting nestlings were small and had orange mouth linings, a yellow gape, and a darker, more sparse coat of down.

We estimated the impact of egg removal by the female cowbird on clutch size of the buntings by comparing the number of eggs in nests with a cowbird egg and in the number of eggs unparasitized nests. We inferred that a lower clutch size of parasitized nests was due to egg removal or damage by the cowbird, as female cowbirds have been seen to remove and eat a host egg before they lay their own (Neudorf and Sealy, 1994; Scott et al., 1992), and they also may damage a host egg when they lay (Payne, 1997; Røskaft et al., 1990).

We determined fledging when the young survived to at least 7 days in the nest. We often heard and sometimes saw birds after they fledged, and in the other cases we confirmed fledging by the form of the nest, when it was stretched and flattened by the growing brood. We determined loss to weather when the nest was found tipped and empty or with abandoned eggs or dead young after a period of wind, cold or rain. We determined predation when the nest that had contained eggs or young was found empty before it could have fledged and the nest was torn or the nest lining was pulled up, much as we observed when we grasped large nestlings and lifted them from the nest (when we observed fledglings out of the nest, the nest was stretched and not torn or lining pulled), excluding loss to weather; we excluded nests ($n = 15$) for which we were uncertain whether the loss was at the egg or the nestling stage. We tested the effect of cowbird nestling competition by comparing the fledging success of buntings in parasitized nests and unparasitized nests when the nest was not predated and at least one young bird, whether bunting or cowbird, survived to fledge from the nest.

We determined postfledging success by observing the buntings when they returned to their natal area in a later year. We banded nearly all nestlings from 1978 through 1990 (a longer period than the study of reproductive success) at day 4–6 when large enough to hold a metal USFWS band and color band (Holcomb, 1966). We did not regularly weigh or measure them to lessen our disturbance to the breeding birds (young 7 days or older sometimes fledged prematurely when an observer approached the nest). In the following years through 1991 we captured and re-marked the banded birds that returned to their natal area (Payne, 1991; Payne and Payne, 1993b). To estimate the effects of competition by fledgling cowbirds, we compared the proportion of nestling buntings that returned in the next year from nests where they fledged with a cowbird and nests where a cowbird did not fledge. Most surviving young apparently settled outside the study area (most new breeding birds in the study area were unbanded when first observed). Nevertheless, the difference in return of parasitized and unparasitized fledglings appeared to be due to survival and not to dispersal: insofar as buntings that fledge from a crowded nest (as with a cowbird) might settle at a distance and be undetected, the observed natal dispersal distances did not vary with brood size of the buntings, and there was no apparent effect of brood competition on natal dispersal distance (Payne, 1991).

We determined the long-term effects of parasitism through the season by comparing the proportion of marked birds that nested again and the success of the next nest when the earlier nest was parasitized and when it was not parasitized. We also compared the total number of buntings fledged for the marked females that were parasitized or were not parasitized in at least one nest.

We determined survival of adults and reproductive success of the adult females into the next year. We interpret whether a bird returned in terms of survival rather than breeding dis-

persal because (1) our survival estimates based on local observations were indistinguishable from continentwide survival estimates based on banding recoveries, (2) our study areas were large enough to detect local movements, and we extended the areas each year through 1984 to control additional local dispersals, and (3) whether an adult settled on its old territory or on a new territory within the study area was independent of its fledging success in the previous year (Payne and Payne, 1990, 1993a, 1996). All females were breeding and banded at a nest, and all males that had a female and were present for at least 28 days in the previous year were included in the analysis. Because both sexes feed the fledged young but the young buntings are often (30%) not fathered by the resident male (Payne and Payne, 1989; Westneat 1988, 1990), we compared adult survival in both sexes but reproductive success only in adult females that returned in a year after rearing a cowbird, or rearing only their own brood, or failing to fledge any nestlings.

Statistical analyses

We compared the proportions of nests parasitized in different habitats and nest plants with log-likelihood G tests and the associations of breeding buntings' age and parasitism with 2×2 chi-square tests. For clutch size, we compared the distribution of numbers with log-likelihood tests, as the clutches were usually zero, three, or four bunting eggs. We used logistic regressions to test whether seasonal variation in clutch size or egg removal by the female cowbirds explained the lower clutch size in parasitized nests.

We used log-likelihood tests to compare the number of buntings fledged in parasitized nests when the cowbird egg failed to hatch, when it hatched but did not fledge, when it fledged, and when the nests were not parasitized. We used t tests to distinguish at which stages the cowbird affected the breeding success of the buntings, and we used the mean differences in success to compare the effects of parasitism at these stages. We determined whether the variances were equal; we report the uncorrected or adjusted t and p values according to the results. We used chi-square and t tests to compare renesting and the breeding success of later nests that followed a parasitized nest and an unparasitized nest. To test whether fledging cowbirds affect the postfledging survival of buntings, we used a chi-square test to compare the proportion of banded nestlings that we saw in a later year. We used one-way ANOVA to compare seasonal reproductive success of females in different categories of being parasitized and t tests to compare these groups pairwise. We used logistic regressions to compare the effects of age, number of buntings fledged, and whether a cowbird fledged on whether a breeding adult bird returned in the following season. We used t tests to compare reproductive success in the next season for females that returned after rearing a cowbird or rearing only their own brood.

Our sample sizes varied with the completeness of the data; for example, we did not always record the nest plant, and not all nests were observed from the time of laying to determine clutch size. We analyzed the two study areas separately because they differed in several features; the consistency in results indicated some generality to the conclusions.

We used the SAS System for Solaris, version 6.11 (Cary, North Carolina), for statistical analyses. All tests were two-tailed and conducted at the $\alpha = .05$ significance level. Means are reported $\pm$ SD.
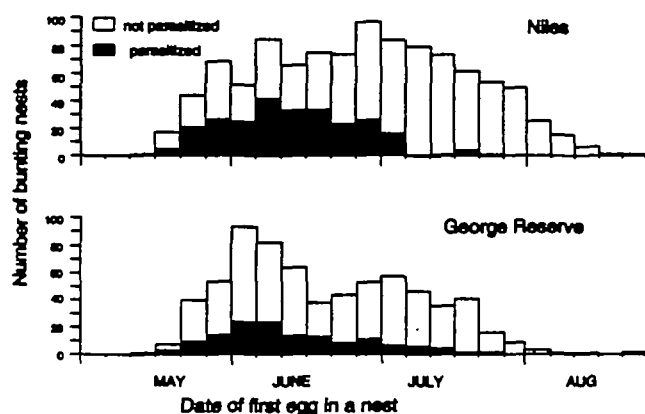
Figure 1
Breeding season of indigo buntings and the seasonal change in incidence of cowbird parasitism.

RESULTS

Risk of cowbird parasitism

Breeding seasons of buntings and cowbirds
Buntings began to nest at the same time in both areas (Figure 1). Mean nest date at Niles (28 June) was a week later than at the reserve (21 June) ($t = 7.62$, $p < .0001$). Mean nest date varied among years (ANOVA, Niles, $F_{1032, 7} = 8.07$, $p < .0001$; George Reserve, $F_{685,7} = 5.08$, $p < .0001$), but the differences were small (≤ 10 days), and the among-years proportion of variance ($r^2 = .05$) was much less than within-years variance. Comparing areas by month, the distribution of nests differed ($G = 47.05$, df = 3, $p < .001$) with more nests of the season in July and August at Niles (46%) than at George Reserve (33%).

The proportion of bunting nests that were parasitized decreased through late spring and summer. At Niles 41% were parasitized in May, 49% in early June, 34% in late June, 11% in July, and none in August. At George Reserve fewer nests were parasitized, with 23% in May, 26% in June, 9% in July, and none in August. Compared by month, the risk of parasitism varied through the season (Niles, $n = 1,040$, $G = 145.7$, df = 3, $p < .001$; George Reserve, $n = 693$, $G = 33.0$, df = 3, $p < .001$). The proportion parasitized did not differ among years (Niles, $G = 5.61$, df = 7, $p = .59$; George Reserve, $G = 8.63$, df = 7, $p = .28$). Through the full breeding season, cowbirds parasitized 26.6% of the nests at Niles, and 19.8% of the nests at George Reserve.

Cowbirds in southern Michigan began to breed a month earlier than buntings and then used other host species, especially song sparrows (*Melospiza melodia*), chipping sparrows (*Spizella passerina*), and field sparrows (*S. pusilla*). The proportion of bunting nests parasitized in the first 2 weeks of their season was as high as in the next few weeks, and sparrows and other small songbirds were also parasitized through the first half of the bunting season. Later in summer the cowbirds quit breeding, while the buntings continued to breed for several weeks. By 20 July, the proportion of bunting nests that were yet to begin in the season was greater at Niles (15%) than at George Reserve (5%), and buntings at Niles were more likely to breed after the risk of cowbird parasitism had passed.

Habitats and nest plants
To test whether risk of being parasitized varied with nesting habitat, we compared the proportion of nests that were parasitized in different habitats (Table 1). The proportion did not differ significantly among these habitats (Niles, $n = 1,040$,

$G = 1.52$, df = 4, $p = .82$; George Reserve, $n = 693$, $G = 4.59$, df = 4, $p = .33$).

Fewer than half the nests were parasitized in each kind of nest plant (Table 2). We found no significant differences among nest plants with at least 10 nests within an area at risk of cowbird parasitism (Niles, $n = 463$, $G = 4.17$, df = 5, $p = .53$; George Reserve, $n = 277$, $G = 6.53$, df = 4, $p = .16$).

Age of breeding adults
In the early nests where eggs were laid by 10 July, yearling and older adult males at Niles were equally likely to be parasitized (yearlings, 39.0% of 213 nests; adults, 34.9% of 505 nests, $\chi^2 = 1.10$, $p = .29$), and at George Reserve the yearling males were more likely to be parasitized (yearlings, 27.5% of 189 nests; adults, 19.8% of 369 nests, $\chi^2 = 4.30$, $p = .04$). At Niles 50 female birds that we banded as nestlings returned in a later year; of those, 28 females that returned as yearlings also returned for a later year, 14 did not return, and 8 we found only in a later year. For these 50 females we found 122 nests. Nests of yearlings were no more likely to be parasitized than nests of older females (yearlings, 56 nests, 35.7% parasitized; older adults, 66 nests, 31.8% parasitized, $\chi^2 = 0.13$, $p > .5$). At George Reserve, where few birds returned to breed in their natal area, 44% of 9 nests were parasitized in the female's yearling year, and 0 of 3 nests in a later year. There was no difference in risk of being parasitized in yearling and older females.

Effects of cowbird parasitism on breeding success

Clutch size
Nests with cowbird eggs had fewer bunting eggs than nests with no cowbird eggs. In the 2 years with our most complete information (Payne, 1992), mean clutch size was significantly lower in the parasitized nests at Niles (unparasitized nests, $n = 174$, $\bar{x} = 3.13 \pm 0.59$ SD; parasitized nests, $n = 97$, $\bar{x} = 2.36 \pm 0.75$; $G = 87.3$, df = 3, $p < .001$) and at George Reserve (unparasitized nests, $n = 87$, $\bar{x} = 3.41 \pm 0.8$; parasitized nests, $n = 37$, $\bar{x} = 2.35 \pm 0.82$; $G = 49.7$, df = 3, $p < .001$).

The difference appears not to be due to female age, as clutch size did not differ between yearling and older females (individual females of each age laid three-egg and four-egg clutches within a season), and both yearling and older females nested through the season (Payne, 1989; our observations). The difference was not due to a larger clutch size after the cowbird season, as mean clutch size of the unparasitized nests (the nests unlikely to have been disturbed by a cowbird) did not increase, rather, it decreased through the first 3 months (Figure 2).

When we considered variables in logistic regressions, whether a nest was parasitized affected clutch size, but month did not at Niles ($n = 271$ nests, month Wald $\chi^2 = 0.22$, df = 4, $p = .64$; parasitism Wald $\chi^2 = 65.6$, $p < .0001$). Both month and parasitism affected clutch size at George Reserve; the effect of parasitism was greater ($n = 124$ nests, month Wald $\chi^2 = 22.4$, $p < .0001$; parasitism Wald $\chi^2 = 44.2$, $p < .0001$).

On the other hand, we observed nests from day to day that lost a bunting egg and gained a cowbird egg. Because age and season did not account for much of the variation in clutch size in the unparasitized nests or for the difference in clutch size between parasitized and unparasitized nests, the difference in clutch size was likely due to a cowbird removing a host egg before she laid her own egg.

Nesting success
Unparasitized nests were significantly more likely to fledge a bunting than were parasitized nests. The unparasitized nests

Table 1

Proportion of nests parasitized in different habitats

| Area | Parasitized? | Habitat | | | | | |
		Edge	Thicket[a]	Swamp	Upland	Woods[b]	Woods[c]
Niles	No	570		39	81	14	59
	Yes	215		10	28	5	19
George Reserve	No	286	88	83	78	23	
	Yes	62	19	26	25	4	

[a] Black locust thicket.

[b] Upland, mainly oak.

[c] Mesic, mainly sugar maple and elm.

were nearly three times more likely to fledge a bunting in both areas (Table 3).

Production of young buntings

Fewer buntings fledged from parasitized nests, and the number fledged varied with the success of the cowbird (Table 4). Comparing all nests, the mean number of buntings fledged was 1.54 ± 1.46 from unparasitized nests and 0.37 ± 0.81 from parasitized nests ($t = 12.3$, $p < .0001$) at Niles, and 1.62 ± 1.51 versus 0.40 ± 0.90 ($t = 16.3$, $p < .0001$) at George Reserve. The cost of parasitism as indicated by the difference in the number of buntings fledged from the parasitized nests was 1.17 fledglings at Niles and 1.22 at George Reserve. The lower success of the unsuccessful nests was often due to loss of the entire clutch or brood to predators or to desertion of the eggs or young, and this affected the buntings as well as the cowbird. Nonetheless, most nests where a cowbird fledged also fledged one or more buntings.

Nest predation

Nests with cowbird eggs and nests with cowbird nestlings were more likely to be taken by a predator than were unparasitized nests. At Niles, 145 (19.3%) of 753 unparasitized clutches and 85 (31.1%) of 273 clutches with a cowbird egg were taken ($\chi^2 = 16.3$, df $= 1$, $p < .001$). At George Reserve, 96 (17.3%) of 556 unparasitized clutches and 39 (28.7%) of 136 clutches with a cowbird egg were taken ($\chi^2 = 9.06$, df $= 1$, $p = .01$). Broods with a nestling cowbird were more likely to be taken than were broods with no cowbird [Niles, 53 of 112 parasitized broods (47.3%), 143 of 626 unparasitized broods (22.8%), $\chi^2 = 29.2$, df $= 1$, $p < .001$; George Reserve, 16 of 44 parasitized broods (36.4%), 106 of 468 unparasitized broods (22.7%), $\chi^2 = 4.17$, df $= 1$, $p < .05$)].

Nestling competition

We tested the competitive effect of cowbird young in nests where at least one nestling (a bunting or a cowbird) survived to fledge. When a cowbird fledged, fewer buntings fledged

(Niles, nests that fledged a cowbird, $n = 45$, $\bar{x} = 1.27 \pm 0.86$ buntings fledged, other nests, $n = 451$, $\bar{x} = 2.71 \pm 0.75$ buntings fledged, $t = 12.2$, $p < .0001$; George Reserve, nests that fledged a cowbird, $n = 29$, $\bar{x} = 0.83 \pm 0.89$, other nests, $n = 325$, $\bar{x} = 2.85 \pm 0.74$, $t = 13.8$, $p < .0001$). In these nests that survived to fledge, the average cost of successful parasitism when a cowbird fledged was 1.44 fewer buntings fledged at Niles and 2.02 fewer at George Reserve.

The effect varied with the number of cowbirds. Three nests fledged two cowbirds, and in these no buntings fledged. No nests fledged three cowbirds; in the two nests with three cowbird eggs, no more than two cowbird eggs hatched. In the 52 nests that fledged both a cowbird and a bunting, most fledged only 1 or 2 buntings, in contrast to the 3 or 4 buntings fledged from nearly all the successful unparasitized nests. In four broods, 3 buntings fledged with a cowbird. In two of these the cowbird hatched after the buntings; hatching time was not determined in the other two. Occasionally ($n = 4$) the cowbird disappeared and the buntings survived to fledge.

Postfledging survival

We observed post-fledging survival when birds banded as nestlings returned to their natal area or were recovered elsewhere in a later year. Of 1413 banded young buntings that fledged at Niles, 125 returned to the study area. Only 1 of 64 buntings that fledged from a nest where a cowbird fledged was seen in a later year—only 1 bunting egg hatched in this nest; she fledged 3 buntings when she returned in her yearling season. In this sample, 9.3% of the buntings that fledged without a cowbird fledging returned, and 1.7% of the buntings that fledged with a cowbird, 18% of the unparasitized rate. Of 1276 young fledged the George Reserve, 27 returned (including 2 recovered elsewhere, Payne, 1991), and none of 32 that fledged with a cowbird. Buntings from nests where a cowbird fledged were significantly less likely to return than were buntings from nests where a cowbird did not fledge at Niles; few birds returned at George Reserve (Table 5). The lower survival of buntings fledged from nests where a cowbird fledged

Table 2

Proportion of nests parasitized in different nest plants

| Area | Parasitized? | Nest plant[a] | | | | | | | | |
		Rubus	Cornus	Bracken	Goldenrod	Gooseberry	Honeysuckle	Multiflora rose	Sapling	Sumac
Niles	No	179	29	5	19	0	2	29	62	10
	Yes	84	11	4	6	2	1	7	20	5
George Reserve	No	72	103	5	6	18	10	10	14	0
	Yes	21	23	1	4	3	0	3	10	0

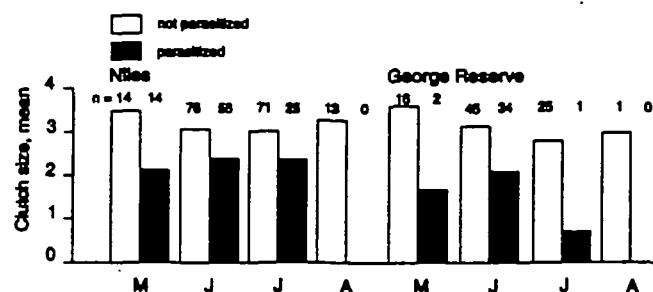[a] Nest plants where $n > 10$ for both study areas combined.

Figure 2
Clutch size of indigo buntings in parasitized and unparasitized nests, from 2 years, where nests were observed from laying (Niles, 1984 and 1985; George Reserve, 1981 and 1982) (Payne, 1992).

may be due to fledging at lower weight or to competition for parental care after fledging.

Although some buntings fledged from nests where a cowbird also fledged, these buntings were rarely recruited into the adult breeding population. The mean fledging success from a nest where a cowbird fledged when adjusted for survival in a later year (18% of the survival of buntings fledged from nests where a cowbird did not fledge at Niles) is 0.22 buntings at Niles and 0.14 buntings at George Reserve, or only 14% of the success of the unparasitized nests at Niles and 12% at George Reserve.

Reproductive success later in the breeding season
Cowbird parasitism is limited to the first half of the breeding season, so to compare the effect of parasitism on later nesting we considered the early nests where an egg was laid by 10 July. For all nests, we found no difference in the proportion of females that nested again (Niles, 63.6% of 632 unparasitized nests were followed by another nest, and 69.5% of 266 parasitized nests, $\chi^2 = 2.92$, df = 1, $p = .09$; George Reserve, 44.7% of 530 unparasitized nests, and 44.1% of 136 parasitized nests, $\chi^2 = 0.02$, df = 1, $p = .90$). For females that nested after their earlier nest had fledged, we found no decrease when they fledged a cowbird (Niles, 59% of 41 nests that fledged a cowbird were followed by another nest, and 44.0% of 164 nests that fledged a bunting but no cowbird, $\chi^2 = 3.05$, df = 1, $p = .08$; George Reserve, 27.6% of 29 nests that fledged a cowbird, and 26.7% of 303 nests that fledged only a bunting, $\chi^2 = 0.01$, df = 1, $p = .92$).

We tested whether the later nest of a female had a lower probability of success when her earlier nest was parasitized (1) in all nests, (2) in nests that fledged a cowbird, and (3) in nests that fledged at least one young, a bunting or a cowbird. If rearing a cowbird affects the ability of a female to rear another brood within the season, then we predict a lower fledging success in nests following a parasitized nest, in scenario 3 and perhaps also in scenario 2. If fledging success depends

on whether the cowbird survives to fledge, then we expect a lower success in scenario 3; if it depends on desertion or other effects of being parasitized, then we expect a lower success in scenario 1 as well. There was no significant decrease in fledging success in later nests that followed a parasitized brood and the clutches and broods that were not parasitized in any of these tests (Table 6).

We also tested whether fewer buntings fledged after the female fledged a cowbird. When she had fledged a nestling of either species, the success of her later nest was slightly lower when a cowbird fledged, but the difference was not significant (Niles, buntings fledged from the early nest, $n = 89$, $\bar{x} = 1.49 \pm 1.45$, cowbird fledged, $n = 14$, $\bar{x} = 1.07 \pm 1.45$, $t = 1.02$, $p = .32$; George Reserve, buntings fledged, $n = 52$, $\bar{x} = 1.73 \pm 1.43$, cowbird fledged, $n = 4$, $\bar{x} = 1.25 \pm 1.50$, $t = 0.62$, $p = .57$). In summary, we found no evidence of decreased breeding success in a later nest after an earlier nest was parasitized.

Seasonal reproductive success
Females that were parasitized fledged fewer buntings than females that were not parasitized (Table 7). At Niles, females not parasitized had the highest reproductive success, but not significantly higher than females whose cowbird fledged ($t = 0.65$, $p = .45$); they had higher success than females whose cowbird failed to hatch or fledge ($t = 4.56$, $p < .0001$). At George Reserve, females not parasitized had higher success than parasitized females, which was significant for females whose cowbird failed and females that fledged a cowbird ($t = 6.65$, $p < .0001$; $t = 2.65$, $p < .01$).

Survival and reproduction in the next season
We tested whether males that fledged a cowbird were as likely to return as were males that did not fledge a cowbird. In logistic regressions, neither male age (yearling or older adult), the number of buntings fledged from all nests on his territory, nor whether a cowbird fledged affected whether the male returned at Niles ($n = 441$, $\chi^2 = 0.69$, df = 3, $p = .87$). Age and number of buntings fledged affected return at George Reserve, but whether a cowbird fledged had no effect ($n = 252$, $\chi^2 = 12.27$, df = 3, $p = .0065$, age Wald $\chi^2 = 4.01$, $p < .05$; buntings fledged Wald $\chi^2 = 4.45$, $p < .05$, cowbird fledged Wald $\chi^2 = 0.38$, $p = .54$).

Female reproductive success affected whether a female returned in the next season, but her minimum age and whether she fledged a cowbird did not (Niles, $n = 433$, $\chi^2 = 20.21$, df = 3, $p = .0001$, buntings fledged Wald $\chi^2 = 17.01$, $p < .0001$; George Reserve, $n = 295$, $\chi^2 = 11.44$, df = 3, $p = .0096$, buntings fledged Wald $\chi^2 = 9.73$, $p = .002$). When the model also included whether a female had fledged any nestling, either bunting or cowbird, the number of buntings fledged was less significant ($p = .06$ at Niles, $p = .03$ at George Reserve) in predicting whether she returned than in the first test, and

Table 3
Nesting success of indigo buntings in unparasitized nests and in nests parasitized by cowbirds

Area	Parasitized?	Success of nests, n (%)		χ^2	df	p
		Fledged a bunting	Did not fledge a bunting			
Niles	No	429 (56.2)	334	101.6	1	<.001
	Yes	58 (20.9)	219			
George Reserve	No	315 (56.7)	241	62.4	1	<.001
	Yes	26 (19.0)	111			

Table 4
Number of indigo buntings fledged in unparasitized and parasitized nests

Area	Cowbird parasitism[a]	Number of nests where *n* buntings fledged					G	df	p
		0	1	2	3	4			
Niles	None	334	23	111	250	45	290.7	12	.001
	Cowbird egg	141	5	4	3	2			
	Cowbird nestling	69	3	3	2	0			
	Cowbird fledged	9	18	15	3	0			
George Reserve	None	241	13	72	178	52	140.1	12	.001
	Cowbird egg	69	1	2	2	2			
	Cowbird nestling	29	0	1	1	1			
	Cowbird fledged	13	9	6	1	0			

[a] Cowbird egg, cowbird egg did not hatch; cowbird nestling, cowbird nestling did not fledge; cowbird fledgling, a cowbird fledged.

the number of buntings fledged and whether a cowbird fledged had no significant effect.

Returning females that had fledged a cowbird fledged as many buntings in the next season as females that had fledged only their own brood (Niles, fledged a cowbird, *n* = 14, $\bar{x}$ = 1.86 ± 1.51; no cowbird, *n* = 146, $\bar{x}$ = 2.10 ± 2.09, *t* = 0.43, *p* = .67; George Reserve, fledged a cowbird, *n* = 6, $\bar{x}$ = 4.00 ± 2.00; no cowbird, *n* = 65, $\bar{x}$ = 2.40 ± 1.96, *t* = 1.95, *p* = .06). We found no decrease in adult survival or reproductive success when the breeding bunting had reared a cowbird in the previous year.

DISCUSSION

Cowbird parasitism of indigo buntings

Indigo buntings are parasitized by cowbirds through their breeding range, and there is no evidence of regional difference in the incidence of brood parasitism where samples were large (*n* > 15) and nests were checked through the breeding season (Table 8). A report of 80% parasitism in Illinois was based on observations in the first half of the breeding season (Robinson, 1992, personal communication; Robinson et al., 1995); later in the season indigo buntings are cowbird-free in Illinois (Twomey, 1945). In Michigan and other parts of the Midwest, parasitism is common early in the breeding season, but cowbirds cease laying by early July (Bent, 1968; Carey, 1982; Johnston, 1964; Lowther, 1993; Payne, 1965, 1976; Peck and James, 1987; Trautman, 1940; Wood, 1951), and the later nests in summer escape parasitism.

Over a longer scale of time, there is little information on the local incidence of cowbird parasitism. However, at George Reserve, from 1934 to 1946, four of nine nests (44%) of indigo buntings were parasitized by 10 July, and none of nine nests were parasitized after 10 July (Sutton, 1959), and the proportion of nests parasitized and the seasonal change in risk of parasitism were like our observations there 40 years later.

Table 5
Postfledging survival of indigo buntings

Area	Buntings fledged seen in later year?	Did a cowbird fledge from the nest?		χ^2	p
		Yes	No		
Niles	No	63	1225	4.41	<.05
	Yes	1	124		
George Reserve	No	32	1217	0.71	ns
	Yes	0	27		

Costs of brood parasitism and costs of defense

Indigo buntings accept the cowbird egg and give care to the cowbird nestling even though cowbird parasitism decreases their own reproductive success. At least half the immediate cost of parasitism can be accounted for by the loss of a host egg when the cowbird lays. At Niles, egg removal accounted for the loss of 0.77 bunting eggs in a nest (the difference in clutch size of unparasitized nests and parasitized nests), and parasitized nests had 1.17 fewer buntings fledged (in all nests, not just those where a nestling fledged); egg removal thus accounted for 66% of the cost of parasitism. At George Reserve, 1.06 fewer bunting eggs were in parasitized nests and 1.22 fewer young fledged from parasitized nests. By this reasoning, egg removal accounted for 87% of the cost of cowbird parasitism.

Nestling competition also is a significant cost of parasitism. In broods that fledged, at Niles 1.44 fewer buntings fledged when a cowbird fledged (twice as many as accounted for by egg removal), and at George Reserve 2.02 fewer buntings fledged when a cowbird fledged (35% more than accounted for by egg removal), so rearing a cowbird to fledge lowered the success of the hosts more than only the losses incurred earlier in the nesting effort. Buntings sometimes starved and died a day or two after hatching when the cowbird was only a day or two older. Cowbirds hatch earlier, are larger at hatching, louder in begging, and grow more rapidly (Morgan, 1976; Ortega and Cruz, 1992; Scott, 1979). Cowbird nestlings were more than 20 g (twice as large as a feathered 10–12 g bunting) and would demand a considerable amount of parental care, as avian energy requirements vary directly with body size (Weathers, 1996). Occasionally a cowbird nestling pushes the bunting nestling from the nest, where it starves (Dearborn, 1996); we observed a few dead nestlings below the nest (one was a second nestling cowbird) while a live cowbird remained in the nest, but we did not directly observe nestling ejection. Buntings grow more slowly in broods with a cowbird nestling than in broods without a cowbird, and more slowly still in broods with two cowbirds, where the buntings starve and fail to fledge (Twomey, 1945). Also, in captive broods the cowbird covered the buntings, pushed them into the floor of the nest, climbed onto them, trampled them, and interfered with their access to feeding (Payne, 1992). The cost of parasitism also includes lower postfledging survival of young buntings, and the buntings that fledged with a cowbird were only 18% as likely to return as buntings from nests where a cowbird did not fledge.

Nests with cowbird eggs were more likely to be taken by a predator, and choice of certain nest sites may have led to discovery both by a cowbird and by a predator. The higher rate of predation of nests with cowbird nestlings may be due to

Table 6

Fledging success in later nest, depending on whether the earlier nest was parasitized

Area	Test[a]	Cowbird parasitism	Success	Buntings fledged (%)	No buntings fledged	χ^2	df	p
				Nest 2 (later)				
Niles	1	Yes	All	38 (50)	38	0.24	1	.62
		No	All	68 (54)	59			
	2		Cowbird fledged	6 (40)	9	0.75	1	.39
			No cowbird fledged	32 (53)	29			
	3		Bunting fledged, no cowbird	49 (58)	36	1.60	1	.21
			Cowbird fledged, bunting ±[b]	6 (40)	9			
George Reserve	1	Yes	All	61 (68)	29	0.06	1	.81
		No	All	13 (62)	7			
	2		Cowbird fledged	2 (40)	3	1.83	1	.18
			No cowbird fledged	11 (73)	4			
	3		Bunting fledged, no cowbird	45 (73)	17	2.35	1	.13
			Cowbird fledged, bunting ±[b]	2 (40)	3			

(Nest 1 (early) columns: Test, Cowbird parasitism, Success)

[a] 1: nest parasitized or not parasitized; 2, 3: all early nests (by 10 July) were parasitized, success of the early nests varied in whether a cowbird fledged.

[b] ± indicates ≥1 bunting either fledged or did not fledge.

the fact that nestling cowbirds are loud, call persistently, and call when unattended. Experimental tests with recorded begging calls in other species indicate that nest predators cue to begging nestlings (Haskell, 1994).

Although cowbirds affect their breeding success, the adult buntings did not remove cowbird eggs nor did they discriminate against cowbird nestlings. The cost of rejecting a cowbird egg may be less than the cost of accepting it. When the host removes an odd egg from the nest, it risks removing its own egg in error or damaging its own eggs (Davies and Brooke, 1988; Davies et al., 1996; Lotem et al., 1995; Røskaft et al., 1990). Many small acceptors such as indigo buntings have short bills and this limits their ability to grasp or pierce the large and hard cowbird egg and remove it from the nest (Rohwer and Spaw, 1988). Also, when the cowbird egg is laid before her own, a bunting may desert at cost, and when it is laid after her own clutch is complete, the cowbird egg may fail to hatch (Payne, 1992). Perhaps a host would not regain the cost already paid when the cowbird removed or damaged a host egg so it will not hatch, and this may explain why most small hosts accept the cowbird egg (Røskaft et al., 1990; Rothstein, 1990). Parental discrimination and rejection of the nestlings in their nest is rare in birds (Davies and Brooke, 1988; Dawkins and Krebs, 1979), and, as with eggs, this lack of discrimination may in part reflect a cost of removing their own young. When we grasped a nestling bunting, it often grasped another nestling or the nest lining, and the disturbance caused another young to leave the nest, either a small nestling that was

accidentally removed or a larger one that prematurely fledged, so the removal of one may lead to the loss of another nestling. In addition, Davies and Brooke (1988) described the difference in removal of a parasitic egg and the removal of a nestling in terms of benefits, where removal of an egg results in the host saving its current brood, but removal of a nestling results in saving only a future brood. This is the argument in cuckoos, where the hatchling evicts the host eggs, and the same may apply to cowbirds where the nestling has already caused the host nestlings to starve.

In summary, the evolutionary response of bunting hosts to cowbird parasitism may be limited by the non-recoverable cost of removal of its egg by the female cowbird, the costs of discriminating eggs and nestlings, and the physical constraints in removing the cowbird egg, all as in some other parasitized songbirds (Davies and Brooke, 1988; Davies et al. 1996; Payne, 1997; Rohwer and Spaw, 1988; Røskaft et al., 1990).

Long-term costs of cowbird parasitism on host survival and reproduction

In our study, cowbird parasitism was independent of the condition of the breeding birds insofar as the probability of being parasitized did not vary with female age or habitat, and cowbird parasitism approximated a natural experiment on the reproductive success of the breeding adults later in the season and in the next season. The subsequent survival and reproductive success of buntings was independent of whether they

Table 7

Seasonal reproductive success of female buntings that were parasitized and those that were not parasitized in at least one nest

Area	Cowbird parasitism	Females n	Buntings fledged $\bar{x} \pm SD$	F	p
Niles	None	337	2.45 ± 1.92	9.37	<.0001
	Cowbird egg, not fledged	144	1.66 ± 1.64		
	Cowbird fledged	35	2.23 ± 1.57		
George Reserve	None	258	2.58 ± 1.85	17.40	<.0001
	Cowbird egg, not fledged	57	1.16 ± 1.36		
	Cowbird fledged	22	1.50 ± 1.63		

Table 8

Cowbird parasitism of indigo buntings in various regions

Region	Parasitized nests/ total nests checked	% Parasitized	Reference
Michigan, Niles	277/1040	26.6	This study
Michigan, George Reserve	137/693	19.8	This study
Michigan, George Reserve	4/18	22	Sutton (1959)
Wisconsin	12/26	46	Young (1963)
Ontario	40/165	24	Peck and James (1987)
Quebec	6/30	20	Terrill (1961)
Ohio	5/16	31	Trautman (1940)
Ohio	17/43	40	Hicks (1934)
Indiana	22/63	35	Carey (1982)
Illinois	16/41	39	Twomey (1945)

reared a cowbird. In this respect, the buntings suffered no long-term cost of rearing a cowbird.

Our observations provide the most comprehensive data on the effect of cowbird parasitism on fledging success for any species of host. Cowbirds affect the breeding success of indigo buntings by means of egg removal, nestling competition, increased risk of nest predation, and decreased survival of young buntings that fledge from a nest where a cowbird also fledges. Because rearing a cowbird to fledging has no effect on a later nest of the adults within a season or on their survival and reproductive success into a later year, the cost of parasitism is mainly accounted for by the frequency of brood parasitism through the breeding season, the difference in fledging success of parasitized and unparasitized nests, and the effect of cowbird fledging on the survival of bunting fledglings. There is little long-term cost of brood parasitism on the reproductive success of adult indigo buntings beyond the impact on their current nest and brood.

REFERENCES

Bent AC (ed), 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. U.S. National Museum Bulletin 237, Washington, DC.

Carey M, 1982. An analysis of factors governing pair-bonding period and the onset of laying in indigo buntings. J Field Ornithol 53:240–248.

Davies NB, Brooke MdeL, 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284.

Davies NB, Brooke MdeL, Kacelnik A, 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. Proc R Soc Lond B 263:925–931.

Dawkins R, Krebs JR, 1979. Arms races between and within species. Proc R Soc Lond B 205:489–521.

Dearborn DC, 1996. Video documentation of a brown-headed cowbird nestling ejecting an indigo bunting nestling from the nest. Condor 98:645–649.

Friedmann H, 1963. Host relations of the parasitic cowbirds. U.S. National Museum Bulletin 233, Washington, DC.

Gustafsson L, Pärt T, 1990. Acceleration of senescence in the collared flycatcher Ficedula albicollis by reproductive cost. Nature 347:279–281.

Gustafsson L, Sutherland WJ, 1988. The cost of reproduction in the collared flycatcher Ficedula albicollis. Nature 335:813–815.

Haskell D, 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proc R Soc Lond B 257:161–164.

Hicks LE, 1934. A summary of cowbird host species in Ohio. Auk 51:385–386.

Högstedt G, 1981. Should there be a positive or negative correlation between survival of adults in a bird population and their clutch size? Am Nat 118:568–571.

Holcomb LC, 1966. The development of grasping and balancing coordination in nestlings of seven species of altricial birds. Wilson Bull 88:57–63.

Johnston RF, 1964. The breeding birds of Kansas. Univ Kansas Publ Mus Nat History 12:575–655.

Lessells CM, 1991. The evolution of life histories. In: Behavioural ecology, 3rd ed (Krebs JR, Davies N, eds). Oxford: Blackwell Scientific; 32–68.

Lessells CM, 1993. The cost of reproduction: do experimental manipulations measure the edge of the options set? Etologia 3:95–111.

Lindén M, Møller, AP, 1989. Costs of reproduction and covariation of life history traits in birds. Trends Ecol Evol 4:367–371.

Lotem A, Nakamura H, Zahavi A, 1995. Constraints on egg discrimination and cuckoo-host co-evolution. Anim Behav 49:1185–1209.

Lowther PE, 1993. Brown-headed cowbird. The birds of North America, no. 47 (Poole A, Gill F, eds). Philadelphia: American Ornithologists' Union.

May RM, Robinson SK, 1985. Population dynamics of avian brood parasitism. Am Nat 126:475–494.

McGillivray WB, 1983. Intraseasonal reproductive costs for the house sparrow (Passer domesticus). Auk 100:25–32.

Morgan FD, 1976. Nesting studies of the indigo bunting (Passerina cyanea) at Thornhill, Indiana. Ind Acad Sci 86:461–465.

Neudorf DL, Sealy SG, 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96:162–169.

Nice MM, 1937. Studies in the life history of the song sparrow. Part 1. Trans Linn Soc NY 4.

Nur N, 1988. The cost of reproduction in birds: an examination of the evidence. Ardea 76:155–168.

Orell M, Rytkönen S, Koivula K, Ronkainen M, Rahiala M, 1996. Brood-size manipulations within the natural range did not reveal intragenerational cost of reproduction in the willow tit Parus montanus. Ibis 138:630–637.

Ortega CP, Cruz A, 1992. Differential growth patterns of nestling brown-headed cowbirds and yellow-headed blackbirds. Auk 109:368–376.

Partridge L, 1989. Lifetime reproductive success and life-history evo-

lution. In: Lifetime reproduction in birds (Newton I, ed). New York: Academic Press; 421–440.

Payne RB, 1965. Clutch size and numbers of eggs laid by brown-headed cowbirds. Condor 67:44–60.

Payne RB, 1976. The clutch size and numbers of eggs of brown-headed cowbirds: effects of latitude and breeding season. Condor 78: 337–342.

Payne RB, 1977. The ecology of brood parasitism in birds. Ann Rev Ecol Syst 8:1–28.

Payne RB, 1989. Indigo bunting. In: Lifetime reproduction in birds (Newton I, ed). New York: Academic Press; 153–172.

Payne RB, 1991. Natal dispersal and population structure in a migratory songbird, the indigo bunting. Evolution 45:49–62.

Payne RB, 1992. Indigo bunting. The birds of North America, no. 4 (Poole A, Stettenheim P, Gill F, eds). Philadelphia: American Ornithologists' Union.

Payne RB, 1997. Avian brood parasitism. In: Host-parasite evolution: general principles and avian models (Clayton DH, Moore J, eds). Oxford: Oxford University Press; 338–369.

Payne RB, Payne LL, 1989. Heritability estimates and behaviour observations: extra-pair matings in indigo buntings. Anim Behav 38: 457–467.

Payne RB, Payne LL, 1990. Survival estimates of indigo buntings: comparison of banding recoveries and local observations. Condor 92: 938–946.

Payne RB, Payne LL, 1993a. Breeding dispersal in indigo buntings: circumstances and consequences for breeding success and population structure. Condor 95:1–24.

Payne RB, Payne LL, 1993b. Song copying and cultural transmission in indigo buntings. Anim Behav 46:1045–1065.

Payne RB, Payne LL, 1996. Dispersal, demography, and the persistence of partnerships in indigo buntings. In: Partnerships in birds: the study of monogamy (Black JM, ed). Oxford: Oxford University Press; 305–320.

Payne RB, Payne LL, Doehlert SM, 1988. Biological and cultural success of song memes in indigo buntings. Ecology 69:104–117.

Peck GK, James RD, 1987. Breeding birds of Ontario, nidiology and distribution, vol 2. Passerines. Life Sciences Miscellaneous Publications. Toronto: Royal Ontario Museum.

Perrins CM, 1965. Population fluctuations and clutch-size in the great tit, Parus major L. J Anim Ecol 34:601–647.

Pettifor RA, 1993. Brood-manipulation experiments. II. A cost of reproduction in blue tits (Parus caeruleus). J Anim Ecol 62:145–159.

Reznick D, 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

Robinson SK, 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. In: Ecology and conservation of Neotropical migrant landbirds (Hagen JM, Johnston DW, eds). Washington, DC: Smithsonian Institution Press; 408–418.

Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J, 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Rohwer S, Spaw CD, 1988. Evolutionary lag versus bill-size constraints:

a comparative study of the acceptance of cowbird eggs by old hosts. Evol Ecol 2:27–36.

Røskaft E, 1985. The effect of enlarged brood size on the future reproductive potential of the rook. J Anim Ecol 54:255–260.

Røskaft E, Orians GH, Beletsky LD, 1990. Why do red-winged blackbirds accept the eggs of brown-headed cowbirds? Evol Ecol 4:35–42.

Rothstein SI, 1975. Evolutionary rates and host defenses against avian brood parasitism. Am Nat 109:161–176.

Rothstein SI, 1990. A model system for coevolution: avian brood parasitism. Annu Rev Ecol Syst 21:481–508.

Scott DM, Weatherhead PJ, Ankney DC, 1992. Egg-eating by female brown-headed cowbirds. Condor 94:585–589.

Scott TW, 1979. Growth and age determination of nestling brown-headed cowbirds. Wilson Bull 91:464–466.

Smith JNM, 1981a. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor 83:153–161.

Smith JNM, 1981b. Does high fecundity reduce survival in song sparrows? Evolution 35:1142–1161.

Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.

Sutton GM, 1959. The nesting fringillids of the Edwin S. George Reserve, southeastern Michigan (part III). Jack-Pine Warb 37:77–101.

Terrill LM, 1961. Cowbird hosts in southern Quebec. Can Field Nat 75:2–11.

Trautman MB, 1940. The birds of Buckeye Lake, Ohio. University of Michigan Museum of Zoology Miscellaneous Publications 44. Ann Arbor: University of Michigan.

Twomey AC, 1945. The bird population of an elm-maple forest with special reference to aspection, territorialism, and coactions. Ecol Monogr 15:173–205.

Verhulst S, Hut RA, 1996. Post-fledging care, multiple breeding and the costs of reproduction in the great tit. Anim Behav 51:957–966.

Weathers WW, 1996. Energetics of postnatal growth. In: Avian energetics and nutritional ecology (Carey C, ed). New York: Chapman and Hall; 461–496.

Westneat DF, 1988. The relationship among polygyny, male parental care, and female breeding success in the indigo bunting. Auk 105: 372–374.

Westneat DF, 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. Behav Ecol Sociobiol 27:67–76.

Westneat DF, Payne RB, Doehlert SM, 1986. Effects of muscle biopsy on survival and breeding success in indigo buntings. Condor 88: 220–227.

Wheelwright NT, Leary J, Fitzgerald C, 1991. The cost of reproduction in the tree swallows (Tachycineta bicolor). Can J Zool 69:2540–2547.

Williams GC, 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690.

Winkler DW, Wilkinson GS, 1988. Parental effort in birds and mammals: theory and measurement. Oxf Surv Evol Biol 5:185–214.

Wood NA, 1951. The birds of Michigan. University of Michigan Museum of Zoology Miscellaneous Publications 75. Ann Arbor: University of Michigan.

Young H, 1963. Breeding success of the cowbird. Wilson Bull 75:115–122.